

NEST SUCCESS AND HABITAT CHOICE OF WILSON'S PLOVERS
IN TOM YAWKEY WILDLIFE CENTER
HERITAGE PRESERVE,
SOUTH CAROLINA

A thesis
Presented to
the Graduate School of
Clemson University

In partial fulfillment
of the Requirements
for the Degree Master of Science
Wildlife and Fisheries Biology

by
Elizabeth Zinsser
May 2013

Accepted by:
Dr. Patrick Jodice, Committee Chair
Dr. Patrick Gerard
Ms. Felicia Sanders

ABSTRACT

Little is known about the reproductive ecology of Wilson's Plover (*Charadrius wilsonia*). I conducted a study of nest site selection and nest success at a critical breeding area in South Carolina, USA. Data from other coastal nesting birds in the region suggest that a suite of environmental factors including flooding and predation may limit nest success in this region. To assess nest success rates of Wilson's Plovers in an area with limited human disturbance I monitored 72 nests during 2012 and 2013 on South Island and Sand Island located in Tom Yawkey Wildlife Center and Heritage Preserve. I measured environmental variables at the micro and macro-habitat scale to assess nest site selection and to determine the effect of habitat characteristics on daily survival rate (DSR) of nests. DSR ranged from 0.969 – 0.988 among both sites and years while the probability of nest survival ranged from 0.405 - 0.764. Daily survival rates were positively related to the density of items (e.g. shells, wood) within 1 m of the nest and negatively related to maximum tide height during the observation interval on South Island. The distance between the nest site and the nearest dune also was related to DSR of nests on South Island but the effect varied between years. Daily survival was higher in 2013 than 2012 on South Island. Survival was not significantly related to any habitat or environmental variables on Sand Island. Flooding, predation, abandonment, wind-blown sand, and a nesting sea turtle were the known causes of nest failure. More research is needed to determine the nest success rates across the region and to determine chick habitat requirements and survival rates.

ACKNOWLEDGEMENTS

First, I would like to thank my academic advisor Dr. Patrick Jodice for all his guidance and support throughout my time at Clemson University. I would also like to thank Ms. Felicia Sanders for her invaluable insight and for her assistance in the field. I would like to thank my committee member, Dr. Patrick Gerard, for his help with my statistical analysis. I am very grateful to the staff of Tom Yawkey Wildlife Center and Heritage Preserve for their logistical support. I would especially like to thank Mr. Jamie Dozier for the opportunity to live and work in such a pristine natural environment, and Mr. Steve Coker for rescuing me upon occasion. Thank you to Mark Spinks for additional logistical support. I would also like to thank Mr. Curtis Walker for his assistance in trapping of Wilson's Plovers.

I would like to acknowledge the USGS South Carolina Cooperative Fish and Wildlife Research Unit, in particular Carolyn Wakefield, for help with a myriad of administrative issues and for general support. This research was supported and funded by the U.S. Fish and Wildlife Service Threatened and Endangered Species Grant Fund and the South Carolina Department of Natural Resources.

Finally, I would like to thank my friends, family, and lab mates for their encouragement throughout this process.

TABLE OF CONTENTS

	Page
TITLE PAGE	i
ABSTRACT.....	ii
ACKNOWLEDGEMENTS.....	iii
LIST OF FIGURES	vi
LIST OF TABLES.....	viii
PREFACE	1
INTRODUCTION	2
METHODS	5
Study Area.....	5
Nest Detection and Nest Success.....	6
Habitat Variables	7
Statistical Analysis.....	9
RESULTS	11
Nesting Chronology and Effort.....	11
Nesting Habitat	12
Causes of Nest Failure	14
Nest Survival.....	15
DISCUSSION	16
Flood Induced Nest Loss	18
Predation Induced Nest Loss	21
SUMMARY AND CONCLUSIONS	25

Table of Contents (Continued)

	Page
APPENDICES	42
Appendix 1	43
Appendix 2	45
LITERATURE CITED	52

LIST OF FIGURES

Figure	Page
1.1 Wilson's Plovers nests were monitored on South Island and Sand Island at Yawkey Center, South Carolina, USA during 2012 and 2013.	27
1.2 Technique used to measure relative nest height. (A) represents a hillock of sand and or debris, (B) represents the location of the nest, (C) represents the marker held horizontal to the ground and (D) represents the ruler held perpendicular to the ground 20 cm from the nest.	28
1.3 Number of nests initiated, hatched and failed by week for Wilson's Plovers nesting at Yawkey Center, South Carolina, USA, March – July 2012 and 2013. Data for both years are combined for each week.	29
1.4 Clutch sizes of Wilson Plovers nesting at Yawkey Center, South Carolina, USA, March – July 2012 and 2013.....	30
1.5 Distance from nest site to nearest dune and relative nest height (i.e., height of nest relative to surrounding ground) for Wilson's Plovers, Yawkey Center, South Carolina, USA, March – July, 2012 and 2013. Bars are mean \pm 1 SE.	31
1.6 Probability of survival across the incubation interval for Wilson's Plovers on South Island, Yawkey Center, South Carolina, USA, March - July 2012 and 2013. Survival probability calculated using results of logistic exposure model. Panel 1- Item density and Distance to dune set at mean, maximum tide height varied from 1.2 m to 1.85 m on 0.5 m intervals. Panel 2- Maximum Tide height and distance to dune held constant at mean, Item density varied from 0 items/m ² to 6 items/m ² on an interval of 0.25 items/m ² . Panel 3- Maximum tide height and item density held constant, distance to dune varied from 1 m to 44 m on 2 m intervals. 2012 represented by grey line. 2013 represented by black line.	32

LIST OF TABLES

Table	Page
1.1 Nesting chronology for Wilson’s Plovers, Yawkey Center, South Carolina, USA, March – July 2012 and 2013.....	34
1.2 Plant presence and absence at nest sites and unused sites on Sand Island at Yawkey Center during 2012 and 2013. Data for 2012 and 2013 are pooled.....	35
1.3 Item presence and absence at nest sites and unused sites on South Island at Yawkey Center during 2012 and 2013. Data are pooled for 2012 and 2013.....	36
1.4 Mean values for parameters that differed significantly between used nest sites and unused sites at Yawkey Center during 2012 and 2013. Relative nest height was tested by sign test, all other variables were tested using a paired t-test Standard errors are included in parentheses. * indicates a significant difference.	37
1.5 Causes of nest loss of Wilson’s Plovers at Yawkey Center, South Carolina, USA March - July 2012 and 2013. Bold numbers indicate primary cause of nest loss for a given site and year.	39
1.6 Significant coefficients from logistic exposure models for Wilson’s Plovers nesting at Yawkey Center, South Carolina, USA, March – July 2012 and 2013. Values in parentheses are standard errors.	40
1.7 Daily survival rate (DSR) and probability of survival for nests of Wilson’s Plovers at Yawkey Center, 2012 and 2013. Standard deviations are included in parentheses. Probability of success is calculated by raising DSR by the number of days included in the laying and incubation periods (29-30 days). DSR was calculated using the coefficients and standard errors from the survival models.	41

PREFACE

The United States Fish and Wildlife Service considers Wilson's Plover (*Charadrius wilsonia*) a species of high concern (Brown *et al.* 2001). The population is estimated to be 8600 individuals in the Southeastern U. S. (Zradkovic 2013). Little research has been conducted on Wilson's Plovers, and no research has been done in South Carolina. Managers lack crucial knowledge related to nesting phenology and habitat use during the nesting and chick rearing phases. Wilson's Plovers are difficult to study due to cryptic nesting habitats, further reducing knowledge of this species.

Specific threats to nesting Wilson's Plovers are similar to those faced by coastal shorebirds in general, and include anthropogenic disturbance at nest sites, vehicular impacts, barrier beach stabilization, and inadequate management on public lands (Brown *et al.* 2001, Melvin *et al.* 1994, Brindock and Brown 2011). Available nesting, chick-rearing and foraging habitat is constrained by disturbance to and development of beach-front areas that would otherwise be suitable for breeding (Corbat and Bergstrom 2000). Of unique concern are research and monitoring efforts associated with sea turtle conservation. For example, field crews operate ATV's in areas that may overlap with nesting and chick-rearing habitat and hence may cause disturbance to breeding birds.

The objectives of this study were to (1) document the nesting phenology of the species at The Yawkey Center, (2) identify micro-habitat features associated with nest placement, (3) measure daily nest survival (DSR) and identify environmental and habitat factors that affect DSR, and (4) identify primary causes of nest failure.

INTRODUCTION

The coast of the Southeastern United States is a critical breeding area for several shorebirds and seabirds (Jodice *et al.* 2007; Hunter 2002). Many of these species are afforded legal protection under state or federal endangered species laws. For example, Least Terns (*Sternula antillarum*), Black Skimmers, (*Rynchops niger*), American Oystercatchers (*Haematopus palliatus*) and Wilson's Plovers (*Charadrius wilsonia*) are listed as threatened or as a species of concern in most southeastern states (Gochfeld and Burger 1994; Thompson *et al.* 1997; Corbat and Bergstrom 2000; Nol and Humphrey 2012). For many of these coastal nesting shorebirds and seabirds, the mechanisms that underlie their relatively low or declining populations appear to be similar. At nest sites, for example, predation pressure and tidal-overwash are frequent causes of low reproductive success for Least Terns, American Oystercatchers, and Black Skimmers in the region (Erwin *et al.* 2001; Thibault 2008; Brooks *et al.* 2013). At a regional scale, increases in the extent and intensity of coastal development, anthropogenic activity, and human disturbance result in a reduction in the quantity and quality of nesting habitat for nesting shorebirds and seabirds and this in turn also appears to have negative effects on reproductive success (Brown *et al.* 2001).

Many declining species, such as those beach-nesting species listed above, experience reduced reproductive success specifically during the nesting phase. Choice of nesting location (i.e., nesting habitat selection) occurs from the landscape to the microhabitat scale and heterogeneity at both levels can play a role in nest site selection (Patten *et al.* 2005; Fedy and Martin 2011). For example, studies have shown that nest

sites of shorebirds differ from non-nest sites in physical and non-physical features across spatial scales and that nest success can subsequently be affected by these differences (Colwell and Oring 1990; Smith *et al.* 2007). At a larger spatial scale, choice of nest sites can be influenced by features such as predator presence, vegetation structure and composition, and proximity to foraging habitat (Tremblay *et al.* 1997; Cohen *et al.* 2009; Miller and Jordan 2011). Features that vary at the microhabitat scale can also affect nest site selection. Nest elevation is important for ground nesting shorebirds, as low-lying nests are vulnerable to flooding (Anteau *et al.* 2012). Shorebirds may choose nest sites that enhance egg crypsis or adult camouflage through substrate heterogeneity or thick vegetative cover; alternatively nest sites with sparse cover can provide the adult an opportunity to visually detect predators (Amat and Masero 2004). Nesting substrate is also important to shorebirds and can mitigate heat stress or predation risk (Saafeld *et al.* 2012). Nests close to vegetation may provide better shelter for chicks but might also be more vulnerable to mammalian predators and areas with lots of litter may provide better camouflage for eggs (Burger 1987). Hence, understanding the factors that affect nest site selection and nest success are critical steps in developing conservation plans.

Wilson's Plovers are listed as a species of high concern by the United States Shorebird Conservation plan (Brown *et al.* 2001). The breeding range for the Wilson's Plover extends along the coast of the southeastern United States from Virginia to Texas and also includes the eastern and western coasts of Mexico and Central America as well as the Caribbean Islands. Wilson's Plovers breed above the intertidal zone in areas with sparse vegetation and feed within the intertidal zone on beaches and tidal mudflats

(Corbat and Bergstrom 2000). Disturbance by humans and livestock, predation, tidal wash-over and abandonment can all reduce nest success of Wilson's Plovers (Corbat and Bergstrom 2000; Ray *et al.* 2011). The population estimate for the species is 8,600 individuals in the southeastern United States but their range is contracting southwards from the historic northern limit in New Jersey (Zdravkovic 2013). The species is state-listed as endangered in Maryland and Virginia, threatened in South Carolina and Georgia, protected in Alabama, and of special concern in North Carolina (Corbat and Bergstrom 2000; Sanders *et al.* 2013; Zdravkovic 2013). A recent survey of all suitable nesting beaches in South Carolina, with the exception of a 4 km stretch at Edingsville Beach, revealed there were Wilson's Plovers present on 40 beaches with an average of 9.5 ± 1.2 pairs per site (Sanders *et al.* 2013). Nesting was most prominent on barrier island beaches (296 pairs, 79%) with the largest concentrations of Wilson's Plovers occurring south of Charleston Harbor at Savannah Spoil Sites, Morris Island, and Kiawah Island. A 2004 survey of Texas recorded 817 pairs (Kolar and Withers 2004). In 2010, 350 breeding pairs were located by a survey of Georgia beaches (Georgia Department of Natural Resources). There are an estimated 160 pairs in Florida (Burney 2009), 240 in North Carolina (Houston and Cameron 2008) and 50 in Virginia (Smith *et al.* 2009).

My goal was to investigate the nesting ecology of Wilsons Plovers, which addresses an important data gap for the species (Zdravkovic 2013). I conducted my study in a core breeding area within South Carolina, The Tom Yawkey Wildlife Center and Heritage Preserve (Yawkey Center) in Georgetown, South Carolina. The Yawkey Center includes undeveloped beach habitat and as such provides a relatively undisturbed system

in which to conduct research. Furthermore, breeding populations in South Carolina have been little studied and information is needed on factors that affect nest success and habitat use for the development of conservation plans. The objectives of this study were to (1) document the nesting phenology of the species at The Yawkey Center, (2) identify micro-habitat features associated with nest placement, (3) measure daily nest survival (DSR) and identify environmental and habitat factors that affect DSR, and (4) identify primary causes of nest failure.

METHODS

Study Area

The Tom Yawkey Wildlife Center Heritage Preserve (Yawkey Center) (33° 15' 03" N, 79° 16' 02" W), a property managed by South Carolina Department of Natural Resources, comprises Cat Island, South Island, Sand Island and North Island (Figure 1). The Yawkey Center is situated between Winyah Bay and North Santee Bay and is separated from the mainland by the Atlantic Intracoastal Waterway. The refuge covers approximately 80 km² and encompasses a variety of habitats including saltwater marsh, managed wetlands, forest openings, longleaf pine forest, maritime forest and ocean beach. Nesting success and habitat use of Wilson's Plovers were monitored on the beaches of South Island (33° 9' 46" N, 79° 12' 19" W) and Sand Island (33° 11' 4" N, 79° 11' 15" W). The beach on South Island is adjacent to maritime forest and has approximately 6.2 linear km of beach-front habitat. The beach on Sand Island is primarily bordered by marsh habitat and has approximately 4.9 linear km of beachfront habitat.

Visitation by tourists is discouraged throughout the summer, however enforcement is inconsistent. Even so, South Island and Sand Island appear to have lower levels of human activity compared to other beaches in South Carolina. Lack of development at Yawkey Center, low accessibility, and restricted access to seabird colonies from April-August combine to provide an essential refuge for nesting shorebirds, wading birds, and near-shore seabirds in South Carolina.

Nest Detection and Nest Success

Nest sites were located by visually searching for Wilson's Plovers that exhibited territorial or nesting behavior. Territorial behaviors included the distraction lure, where plovers conspicuously run away from nest sites, mates, or chicks, to draw predators away; the "tweet" call, a long clear whistle that slides upwards in pitch at the end; the "rattling" call, a hard, short, rattle; and the wing drag, where a plover acts as if its wing is broken to distract a predator from a nest site or chicks (Bergstrom 1988). Nesting behaviors included scraping, making a depression by vigorous kicking of the feet; marking time, the male stands in front of the female and kicks his feet; mounting; and copulation (Bergstrom 1988). Once nesting or territorial behavior was identified I scanned the ground for tracks and followed them until nest sites were located. Nests were marked using surveyor flags placed 1 m from the nest. The lay date of the first egg was recorded whenever possible and potential hatch date was calculated as 25 days from the date the third egg was laid (Tomkins 1965). In the event the clutch was found after completion an egg was floated to estimate lay date (Mabee *et al.* 2006).

I monitored nest survival by visually checking nests every 3 ± 1.3 days on average (range 1 – 5 d). A nest was considered successful if ≥ 1 egg hatched. I considered a nest hatched if (1) newly hatched chicks were observed within 20 m of the nest site, or (2) eggs were no longer present near the anticipated hatch date and parents exhibited defensive behavior in the vicinity of the nest. If an empty nest was encountered at the time of hatch but the parents failed to act defensive the nest was considered to have failed. Nests were defined as flooded when eggs were absent from a nest immediately following a spring-tide which also deposited wrack or debris in the vicinity of the nest. Nests were considered abandoned after three consecutive nest checks without sign of parents. Nests were categorized as predated when a nest disappeared at a time other than near the anticipated hatch date in the absence of flooding events and if predator tracks or signs also were present. Six RECONYX trail cameras were deployed opportunistically at nests on Sand Island and South Island in 2012 and 2013. The fate was considered undetermined if there were no signs of hatching, there had been no extreme weather events or signs of flooding, and there were no signs of predation.

Habitat Variables

Nest site coordinates were recorded using a handheld GPS to ± 3 m. I recorded the following habitat characteristics on the day the nest was detected; distance from nest to the nearest dune with a height greater than 1.5 m; distance from nest to the nearest plant greater than 10 cm in height with an area at least 0.25 m^2 ; and distance from nest to the high-tide line and the height of the nearest plant from the ground to the tip of the nearest

stem (plant height). I measured the distance from the nest to each habitat feature using a tape measure. I chose these variables in part based on their biological relevance in previous studies on Wilson's Plovers (Dikun 2008; Ray 2011). Distances between the nest and either the nearest dune or plant changed little if at all throughout the season but were not measured regularly to decrease time spent in the vicinity of the nest. However, I also include a measure of maximum tide height during the observation interval to assess the effect of tide on nest success

(<http://tidesandcurrents.noaa.gov/noaatidepredictions/NOAATidesFacade.jsp?Stationid=TEC2929>). I also centered a 1 m² quadrat on the nest and counted all shells and other items larger than 1.5 cm in diameter (pooled as a single category, items), sticks longer than 10 cm, and any live plant stems within the plot. Items and plants were recorded both as presence/absence and as items/m² and plants/m². Items within the quadrat appeared relatively constant throughout the nesting period and were only counted once to minimize disturbance. The height of the nest relative to the adjacent ground was measured holding a ruler perpendicular to the ground 20 cm from the nest center and a marker was held parallel to the ground so that the ruler was held parallel to the ground at the same height as the eggs. The height at which the marker intersected the ruler was recorded as the height of the nest (Figure 2).

An unused site was chosen five meters away from each nest location in a randomly chosen direction to assess microhabitat features. Using a randomly chosen direction in combination with a fixed distance is a common approach for microhabitat selection studies (Compton *et al.* 2002; Fedy *et al.* 2011). By using a fixed distance I

ensured that the unused location was within the territory of the Wilson's Plover pair I was observing at the time and within the same patch of habitat as the nest site. A one-meter square quadrat was placed so that the center of the quadrat was five meters away from the used site and the microhabitat variables described above were measured (i.e. number of shells, driftwood pieces and plants, and relative height). The distance from nearest plant to the unused location was measured and the height of the nearest plant was measured. Measurements at the unused location were collected on the same day as the measurements at the nest site.

Statistical Analysis

I used ANOVA to determine if any of the habitat variables I measured (initiation date, midpoint, distance to dune, height of vegetation, distance to vegetation, distance to high-tide line, item density, and number of plants) differed between South and Sand island or between study years. Because there was a significant difference for several variables between the two study sites (see Results) all-subsequent analyses were conducted separately by site. I used an exact binomial proportion test to determine if there was a difference between the number of nests with three egg clutches compared with the number of nests with one and two egg clutches.

I modeled daily survival rate (DSR) of Wilson's Plovers using a logistic exposure model (Schaffer 2004). I followed a backwards elimination technique using a *P*-value of 0.15 for selection purposes. I also assessed multicollinearity of continuous independent variables with a correlation analysis and avoided pairing any strongly correlated terms (*r*

> 0.60) in the same model. Independent variables for the DSR model included item density and live plant density within the nest quadrat, distance to the nearest plant, dune and the high-tide line, height of the nearest plant, initiation date, midpoint ((date of last observation-initiation date)/2), midpoint², maximum tide height during the observation interval, and exposure days (the number of days a nest existed).

The logistic exposure model is composed of three expressions: (1) a probability distribution of the binomial response, (2) a predictor function of the explanatory variables (expression 1), and (3) a link function that relates component two to component one (expression 2) (Schaffer 2004). Let t equal the length of the observation interval (days) for a nest. The probability the nest will survive the interval is $\theta = s^t$ where s equals the daily survival rate dependent on the value of the explanatory variable x (Schaffer 2004). The probability of survival across the entire incubation interval is equal to DSR raised to the power of incubation days (Lloyd and Tewksbury 2007).

$$s(x) = \frac{e^{\beta_0 + \beta_1 x}}{1 + e^{\beta_0 + \beta_1 x}} \quad (1)$$

$$g(\theta) = \log_e \left(\frac{\theta^{\frac{1}{t}}}{1 - \theta^{\frac{1}{t}}} \right) \quad (2)$$

The data were underdispersed for both sites (Sand deviance/DF = 0.54 South: deviance/DF = 0.36) so we used a liberal alpha value of 0.15 during the backwards elimination process. The alpha level was set at 0.10 to determine explanatory variable significance for all analyses.

I modeled micro-habitat characteristics at nest sites and unused sites to assess nesting habitat selection. I used McNemar's test to test the hypothesis that there was no

difference in the proportion of nest sites that contained ≥ 1 plant or item and the proportion of unused sites that contained ≥ 1 plant or item. A *P*-value of 0.10 was used to determine significance.

I used a MANOVA to assess the relationship between micro-habitat variables that were measured on a continuous scale (i.e., item density, plant density, distance to nearest plant, plant height, and relative nest height) and the differences in those values between nest sites and unused sites. The difference between the values at nest sites and unused sites was calculated for each habitat variable and used as the response variable. Because the MANOVA returned a result that indicated significant differences for at least one habitat parameter, I ran a series of paired t-test on the values for item density, plant density, distance to nearest plant and plant height. I ran a sign test to compare relative nest height at nest sites and unused sites because those data did not display a normal distribution. I used a *P*-value of 0.10 for the MANOVA, the paired t-tests, and the sign test to determine significant differences.

Mean values are reported ± 1 standard error. All analyses were done using SAS 9.3 (SAS institute, Cary, North Carolina).

RESULTS

Nesting Chronology and Effort

During 2012 I located 22 nests on South Island and 17 nests on Sand Island, and during 2013 I located 16 nests on South Island and 17 nests on Sand Island (Appendix 1

and 2). Wilson's Plovers nested in three types of habitat: (1) strand ($n = 1$ nests on Sand Island and 15 nests on South Island), the stretch of beach between the dunes and the high tide line, (2) dunefield ($n = 0$ nests on Sand Island and 23 nests on South Island), the area behind the primary dune line characterized by sparse vegetation and dunes oriented in any direction compared to the nest site, and (3) immature dune ($n = 33$ nests on Sand Island and 0 nests on South Island), characterized by sparse dunes ≤ 2 m tall. Plovers did not nest below the average high tide line or on the exposed sand bar at the north end of South Island. Nests initiated 15 days earlier ($F_{3,68} = 3.34$, $P = 0.02$) on South Island (26 April ± 22.1 days) compared to Sand Island (11 May ± 23.5 days). Nesting began on 30 March and lasted for 103 days in 2012. In 2013 nesting began on 2 April and lasted for 96 days (Table 1). Hatching began in late April in 2012 and early May in 2013. Nesting extended through early July in both seasons but was most frequent in April and May; chick rearing continued through mid-August (Figure 3).

The average incubation length of Wilson's Plovers on Sand Island was 27 ± 5.7 days and 30 ± 1.1 days in 2012 and 2013, respectively. The average incubation length on South Island was 29 ± 1.4 days and 30 ± 1.7 days in 2012 and 2013, respectively. Three-egg clutches predominated compared to one and two egg clutches on both South Island ($\chi^2_1 = 6.5$, $P_{2012} = 0.02$; $\chi^2_1 = 6.2$, $P_{2013} = 0.02$) and Sand Island ($\chi^2_1 = 7.1$, $P_{2012} = 0.01$; $\chi^2_1 = 7.1$, $P_{2013} = 0.01$) during 2012 and 2013 (Figure 4) and comprised 77% - 82% of clutches among sites and years.

Nesting Habitat

Prior to assessing habitat selection or estimating DSRs, and as a means to rule out confounding relationships among habitat and study sites and years, I examined the relationship between habitat characteristics at nests and site (South Island or Sand Island), year (2012 or 2013), and site*year. Several habitat characteristics at nest sites differed between South Island and Sand Island suggesting results could be confounded if data were pooled among islands. The density of items at the nest site was greater ($F_{3,68} = 7.3$, $P < 0.01$) on South Island (17.8 ± 15.1 items/m²) compared to Sand Island (4.9 ± 5.6 items/m²). The vegetation was taller ($F_{3,68} = 3.7$, $P = 0.01$) on South Island (68.4 ± 37.3 cm) compared to Sand Island (48.0 ± 21.0 cm). Vegetation was further ($F_{3,68} = 3.53$, $P = 0.06$) from nests on Sand Island (607.9 ± 96.3 cm) than South Island (335.9 ± 37.2 cm). There was a significant interaction of site and year on both distance to dune ($F_{3,68} = 6.5$, $P < 0.01$) and relative nest height ($F_{3,68} = 3.0$, $P = 0.04$; Figure 5). The distance to dune appeared to be greatest on Sand Island in 2012 (27.3 ± 6.3 m) and lowest on South Island in 2012 (5.1 ± 1.1 m). Relative nest height appeared greater on Sand Island in 2013 (3.7 ± 0.8 cm) and lowest on South Island in 2013 (1.2 ± 0.6 cm). There were no significant site or year effects ($P > 0.10$ for each) on plant density (5.0 ± 1.3 plants/m²) or the distance from the nest site to the high tide line on the day the nest was found (4.6 ± 3.6 m). Nonetheless, due to the significant site differences in five of the eight habitat variables I measured, all subsequent analyses were conducted separately by island.

I compared microhabitat features at nest sites and paired unused sites and found significant differences for several habitat variables (i.e., the presence or absence of items, and the presence or absence of plants). The probability of plants occurring at nest and

unused sites was not the same on Sand Island (McNemar's $P = 0.01$). In 29.4% of 34 pairings, plants were present at the nest site but not the unused site. Plants were absent at both nest and unused sites in 58.8% of 34 pairings. Plants were never present at both the nest site and unused site, nor were plants ever present at the unused site but absent at the nest site (Table 2). On South Island the probability of finding items in the quadrat was not the same at nest and unused sites (McNemar's $P = 0.03$). Items were present at the nest site but not the unused site in 31.6% of 38 pairings. Items were absent from both the nest site and unused site in 0.5% of 38 pairings and present in both nest and unused sites in 55.3% of 38 pairings (Table 3).

The results of a MANOVA assessing the relationship between habitat factors measured as continuous variables (i.e., item density, the plant density, the distance to nearest vegetation, the relative height, and the vegetation height) at nest and unused sites showed several differences on both South Island ($P < 0.01$) and Sand Island ($P < 0.01$). Paired t-tests subsequently revealed that item density ($t_{37} = 2.67$, $P = 0.01$) and distance to nearest vegetation ($t_{37} = 2.93$; $P < 0.01$) were greater for nest sites compared to unused sites on South Island (Table 4). The sign test revealed that relative nest height was significantly greater for nest sites compared to unused sites ($P \leq 0.01$) on South Island (Table 4). On Sand Island, plant density ($t_{33} = 1.9$, $P \leq 0.07$; Table 4) and relative nest height were greater at nest sites compared to unused sites ($t_{33} = 4.8$, $P \leq 0.01$; Table 4) and plant height was lower at nest sites compared to unused sites ($t_{33} = -2.6$, $P = 0.01$; Table 4).

Causes of Nest Failure

Of the 72 Wilson's Plovers nests detected, 42% of those on South Island (n=17) failed and 53% (n=19) of those on Sand Island failed. Flooding was a primary cause of failure on both South Island (45%) and Sand Island (27%) during 2012 but did not occur on South Island during 2013 (Table 5). Flooding on Sand Island was the primary cause of failure in 2013 (67%) but cause of nest failure was difficult to determine during 2012 (45% failed due to unknown causes). Predation caused 50% of failure on South Island during 2013 (Table 5). One predation event was confirmed by photographic evidence; at 21:31 local time on 11 May 2012 a bobcat (*Lynx rufus*) consumed all eggs at nest SND1210 (Appendices 1 and 2) on Sand Island. Nest abandonment occurred on South Island but was not recorded on Sand Island. Two nests were assigned a failure category of "other". In 2012 a nesting sea turtle destroyed a nest on Sand Island (SND1214, Appendices 1 and 2), and in 2013 a nest on South Island was buried by windblown sand (STH1302, Appendices 1 and 2).

Nest Survival

I monitored 38 Wilson's Plover nests on South Island over 302 observation intervals during 2012 and 2013. The most parsimonious model for DSR of nests on South Island included item density, distance to dune, maximum tide height, and year as explanatory terms (Table 6). DSR of nests was higher in 2013 compared to 2012 and the odds of a nest surviving increased by 3.5 times during 2013 on South Island. DSR was negatively related to maximum tide height, positively related to item density and negatively related to distance to dune (Figure 6). I monitored 34 Wilson's Plovers nests

on Sand Island over 202 observation intervals during 2012 and 2013. The backwards selection process eliminated all predictor variables from the model of DSR from Sand Island indicating that none of the variables I measured had a significant relationship with DSR (Table 6).

Because there was a significant year effect on DSR of nests at South Island I estimated nest survival and the probability of nest success separately by year there (Table 7). The DSR for nests was 0.977 in 2012 and 0.988 in 2013 at South Island. The probability of a nest surviving from laying to hatching was 56.1% in 2012 and 76.4% in 2013 at South Island. The DSR and probability of success at Sand Island for both years combined was 0.969 and 40.5%, respectively (Table 7).

DISCUSSION

Nest success is often variable within sites and among years as well as between proximate sites within years for beach-nesting birds in the southeastern United States (Corbat 1990; Thibault 2008; Brooks 2011). Daily survival rate of nests of Wilsons Plovers did not appear to be consistent among sites and years. The probability of a nest succeeding at South Island was greater than 50% in each of my two study years (and as high as 76%) while at Sand Island the probability of a nest succeeding was only 40%. Mayfield estimates of nest success for Wilsons Plovers in North Carolina were 46% in 2008 and 44% in 2009 (Ray 2011). Wilson's Plovers in Louisiana in 2007 had a nest success of 58.0% when calculated by logistic regression (Zdravkovic 2010). Apparent

nest success was as low as 0% and as high as 31% with an average of 8.6% in Georgia between 1986 and 1987 (Corbat 1990). Apparent nest success in Texas ranged from 25.0% to 53.8% during 1988 and 66% in 2005 (Bergstrom 1988; Zdravkovic 2005). While caution must be used when comparing nest success calculated using different methods, the Wilson's Plovers at Yawkey Center appear to have average to above average nest success during the two years of my study when compared to other studies in the southeastern United States.

There were habitat differences on South Island compared to Sand Island that may have contributed to the apparent differences in DSR. For example, Sand Island appears to have a lower profile than South Island and subsequently appears to also experience more frequent washover events compared to South Island. The washover regime on Sand Island appears to prevent the complete formation of barrier dunes, which are present on South Island. Because of this inherent difference in beach structure, nests on Sand Island were primarily found in areas characterized by sparse dunes ≤ 1.5 m in height while nests on South Island were either behind a well-established dune line or along the strand. It appears that increased washover at Sand Island creates a more open habitat, which may contribute to the slightly greater distance between nests and dunes and between nests and vegetation on Sand Island compared to South Island. While the distance between nests and dunes on Sand Island appeared to be less in 2013 compared to 2012 it still appeared to be greater than the distance between nests and dunes on South Island in both years. The increased plant height observed on South Island may be attributed to a difference in vegetation composition; there appeared to be more sea oats present on South Island than

Sand Island. Nests that were close to sea oats would have had taller vegetation than those that were close to other species of plant, thereby increasing that average plant height on South Island compared to Sand Island. Therefore, despite a small spatial separation between the islands, habitat factors differed significantly between islands suggesting that nesting ecology at nearby sites may not always be similar.

Flood Induced Nest Loss

Flooding accounted for 27-67% of identified nest loss in three out of four site-years. Flooding also was an important cause of nest failure for Wilson's Plovers in Georgia (Corbat 1990). During my study, flooding occurred during extreme spring-tide events during the 2012 breeding season, one on 6 April and one on 6 May; the full moon coincided with easterly winds, which drove water into areas behind the primary dune during both April and May. One spring tide event also affected Sand Island in 2013. During spring-tide events, nesting areas were completely inundated by water, likely contributing to the high number of nest failures. These acute events appeared to affect nest success on Sand Island more than on South Island, and may have masked any impact of daily high tides as observed on South Island. Flooding from daily high tides is a common cause of nest failure among other beach nesting birds in the region including Least Terns, American Oystercatchers and Black Skimmers (Thibault 2008; Brooks *et al.* 2013).

No flood induced nest loss occurred on South Island in 2013. The lack of flooding on South Island in 2013 could have been caused by a site-wide delay in nest initiations.

Although nest initiation was not significantly later in 2013 compared to 2012, there may have been an important environmental difference. In 2013 nest initiation began only 7 days later than 2012, but that shifted nesting primarily after the April spring tide-event. The slight delay in nest initiation in 2013 therefore may have contributed to fewer nests failures due to flooding. An explanation for the site-wide delay in nesting during 2013 could be the decreased temperatures in 2013 compared to 2012. There were a total of 63 heating-degree days during March and April during 2012 and there were 233 heating-degree days in 2013 (<http://www.weatherdatadepot.com>). Wilson's Plovers began nesting in late March and early April; the delayed nesting in 2013 could have been a result of the cooler temperatures. Avian reproduction is known to be tightly correlated with environmental cues, including temperature. An experiment with Great Tits (*Parus major*) showed that females timed incubation with increasing temperatures, though there appeared to be a genetic influence on timing as well (Schaper *et al.* 2012).

There was a positive relationship between survival probabilities when nests were located closer to the dune on South Island. Nests were found both within the dunefield and along the strand. Nests in the dunefield were not always located between the ocean and the dune; rather the nearest dune could be located in any orientation relative to the nest and the ocean. As distance to dune decreased, elevation relative to sea level may also have increased, thereby decreasing the risk of flood induced nest loss. Three of the nests on South Island were located directly on a dune slope, which obviously increased their elevation compared to nests that were not located on dune slopes. Nests that were close to the dune, but not on the slope of the dune, may have benefitted from the relative elevation

difference between the dunefield and the intertidal zone. Least Terns also choose nest sites placed intermediately between dunes and the high tide lines to reduce the risk of flooding (Burger and Gochfeld 1990) and Piping plovers have also been shown to nest closer to dunes than the high tide line (Burger 1987). Slight elevation differences caused by small (<10 cm) hillocks of sand may also have reduced risk of flooding. Wilson's Plovers on South Island and Sand Island used nest sites that had greater relative elevation compared to unused locations. Areas of relatively increased elevation appeared to be rare on both islands and none of the unused locations had increased elevation relative to the ground around them. This indicates that Wilson's Plovers may be choosing areas that increase their relative nest height at a micro-habitat scale. Considering the proportion of nests that failed due to flooding, choosing areas with even a slight increase in elevation compared to the surrounding ground may increase nest survival. When areas flooded, the water was often shallow enough that slight elevations, such as those that Wilson's Plovers nested on, remained dry. Nests on these hillocks of sand did not fail due to flooding, while nests on the bare ground were often washed away.

Flooding caused more nest loss on Sand Island (45% in 2012 and 2013) than South Island (29% in 2012 and 2013) and yet neither maximum tide height nor any of the other variables I measured were significantly related to nest survival on Sand Island. Therefore, it appears that DSR on Sand Island could have been affected by a variable not measured during the course of this study. Sand Island has a low profile, no protective barrier dune, and is neighbored by marsh and tidal creeks to the west, which seems to render it more prone to flooding than South Island. Nest elevation relative to sea level

may have had an impact on survival. The topography of Sand Island may have made it more susceptible to flooding. Flooding appeared to be more prevalent in the area close to the tidal creek than the area near the jetty, which is located at the northeastern end of the study area on Sand Island. It is possible that an elevation gradient existed which protected nests close to the jetty. Flooding was not the only cause of failure on Sand Island and it is possible that the factors influencing the probability of survival were not reflected by the data I collected. Other factors, such as nest proximity to foraging grounds or predation pressure may have a greater effect on nest success there (Smith *et al.* 2007).

Predation Induced Nest Loss

Predation caused frequent failures on both Sand Island and South Island. Nest loss to predation is common among the sea and shorebirds of the southeastern United States (Bergstrom 1988; Corbat 1990; Thibault 2008; Brooks 2011). Ghost crabs (*Cancer ceratophthalmus*), coyotes (*Canis latrans*), bobcats, raccoons (*Procyon lotor*), opossums (*Didelphis virginiana*) and avian predators were present on both islands and could have been responsible for predation events. For example, coyote and ghost crab tracks were observed in nest cups of failed nests of Wilsons Plovers during my study. Coyote and raccoon populations are controlled at Yawkey Center to protect the nesting sea turtle population; however control does not completely prevent depredation of nests of shorebirds or loggerhead sea turtles (*Caretta caretta*). Several plover nests failed due to unknown causes during 2012 and 2013; it is possible that some of the unknown nest failures were actually predation events. Existing signs of predation could have been

obscured by wind-blown sand or obliterated by rain, and avian predators are notoriously difficult to detect (Williams and Wood 2002; Brooks 2011). A robust experiment including remote cameras may provide additional data on the rate, type, and timing of predation at nest sites.

One factor that may have influenced predation pressure on nests was the item density in the nesting quadrat. There was a positive relationship between DSR of nests and the density of items at the nest site on South Island. Wilson's Plover eggs are buff colored with dark brown markings, a color scheme which is common among ground-nesting birds to enhance egg crypsis (Smith *et al.* 2012). An increase in the debris near the nest site may have provided better camouflage, which subsequently may have increased DSR. Nests on South Island also had a higher density of items in the nest quadrat, were further from plants, and had a greater relative height than paired unused sites. Item density was also positively related to nest success. Therefore, Wilson's Plovers nests on South Island were in areas with more items than the paired unused site and had higher success in nest sites with more debris in the quadrat. There was more debris in nest quadrats on South Island than on Sand Island. There were more plants in the nest quadrat than nearby unused sites on Sand Island compared to South Island. It is possible that the plants on Sand Island acted as nest site camouflage as the items inside the quadrat did on South Island. These observations support the hypothesis that debris around the nest site increases nest crypsis (Smith *et al.* 2012). If increased nest site debris increases survival, then we may expect predation rates to be higher at nests with low levels of nest debris, something that warrants further testing at Yawkey Center (Saalfeld

et al. 2012). The positive relationship I observed between DSR and item density near the nest is, however, in contrast with a study on Snowy Plovers in Texas where there was no relationship between substrate heterogeneity and nest survival (Saalfeld *et al.* 2011). Past studies have shown that nests located on heterogeneous substrates experienced lower predation rates compared to nests on homogenous substrates, like sand (Page *et al.* 1985). Semipalmated Plovers (*Charadrius semipalmatus*) in Nunavut selected nesting sites with a higher percentage of pebble cover, however individuals nesting in areas with high pebble cover were not more successful (Nguyen *et al.* 2003). The relationship between nest site camouflage and nest success is therefore inconsistent among this suite of related species. Wilson's Plovers had higher DSR when the density of items at the nest site was high but it may not have been as a result of increased egg crypsis. Instead, the increased density of items present near the nest could have been an indication the nest site was more protected from tidal flooding and blow-over sand, both of which were causes of failure.

The relationship between distance to dune and survival probability could have played a roll in protecting nests from predation as well, resulting in increased survival for nests closer to dunes. Little Terns (*Sternula albifrons*), a species of bird that nests in similar habitat compared to Wilson's Plovers, had higher nest success when they nested closer to dunes than the ocean (Medeiros *et al.* 2012). Since conspicuous nests may have lower nest success (Medeiros *et al.* 2012), birds that nest near structures that obstruct a predator's view may experience lower predation rates. Wilson's Plover nests that were closer to the dune may have had increased camouflage from predators than nests further

from the dune. At least five nests on Sand Island failed due to predation and Sand Island has an open profile due to lack of dunes and high distance to vegetation. It is possible that the lack of visual obstructions on Sand Island contributed to predation events. Survival may even have been positively impacted by a combination of decreased distance to dune and increased nest site debris. A study on Piping Plover nest lining showed that debris increased as distance to dune decreased (Greenwald *et al.* 2009) and DSR of Wilson's Plovers on South Island was increased with an increase in items in the quadrat. If the density of items increased as the distance to dune decreased, then nests close to the dune may have been better camouflaged. Wilson's Plovers rely on cryptic nest placement to increase nest success (Corbat 1990) and nests that were close to the dune may have been obscured from view by increased vegetation presence or increased debris.

SUMMARY AND CONCLUSIONS

Ecological stressors that suppress nest success or alter habitat choice during nesting have the potential to affect population levels over the long term (Julliard 2004; Norris *et al.* 2004). Flooding, predation, anthropogenic habitat modification, and human disturbance by tourists and conservationists are all factors that affect reproductive ecology of shorebirds in the southeastern United States (Cohen *et al.* 2009; Ray 2011; Brooks *et al.* 2012). Wilson's Plovers nesting in South Carolina are vulnerable to these stressors but little is known about specific effects. I measured nest success and habitat use of Wilson's Plovers in Tom Yawkey Wildlife Center and Heritage Preserve in Georgetown, South Carolina to better understand their biology and the effects of environmental factors on nesting success.

Wilson's Plovers' nest sites were significantly different than unused sites on both South Island and Sand Island. Nest sites had a higher item density, were further from vegetation, and had a greater relative height than unused sites on South Island. Nest sites had a higher plant density, were close to shorter plants, and had a greater relative nest height than unused sites on Sand Island. Relative nest height was greater at nest sites than unused sites at both islands. The increased elevation was caused by small ($\leq 10\text{cm}$) hillocks of accumulated sand and vegetation. The hillocks were sparsely distributed and no unused sites contained these structures, so it is possible that Wilson's Plovers were specifically choosing them.

Wilson's Plovers in Yawkey Center had variable nesting success between sites and years. The probability of survival was highest on South Island in 2013 and lowest on

Sand Island. The probability of survival was positively related to the density of items such as shell fragments at the nest site, negatively related to maximum tide height during the observation interval, and negatively related to the distance between the nearest dune and the nest site on South Island. The relationship between maximum tide height and nest survival reflects the number of flood-induced failures on South Island in both 2012. The flood-induced failures occurred during spring tide events during 2012 where multiple failures occurred at the same time. The probability of survival was not significantly related to any of the habitat or environmental variables measured on Sand Island. It is possible that the habitat is homogenous enough that a non-habitat related factor is affecting nest success on Sand Island. Predation occurred on both islands but predation pressure was not measured directly.

Flooding occurred in three out of four site years during the course of my study. While this study was only of short duration, it is possible that flooding is an important factor determining nest success in Wilson's Plovers. Flooding in the nearby Cape Romain National Wildlife Refuge similarly affects American Oystercatchers, Black Skimmers, and Least Terns (Thibault 2008; Brooks 2011). Flooding may continue to be an issue for Wilson's Plovers due to predicted sea-level rise and it will be exacerbated because habitat availability is circumscribed by human modification. Predation was also a cause of failure for Wilson's Plovers, as it is for other seabirds in the region. Invasive predators and high abundances of native predators exist throughout the southeastern United States. Managers charged with promoting nest success should be aware of the threats posed by predation and flooding.



Figure 1. Wilson's Plovers nests were monitored on South Island and Sand Island at Yawkey Center, South Carolina, USA during 2012 and 2013.

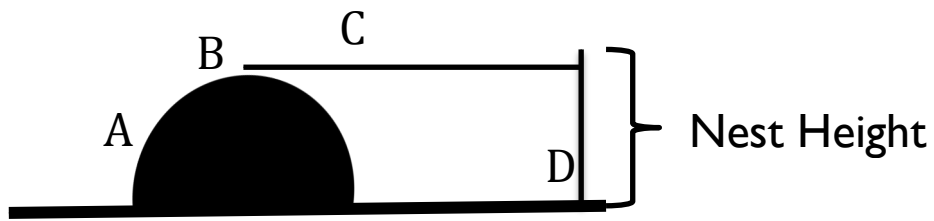


Figure 2. Technique used to measure relative nest height. (A) represents a hillock of sand and or debris, (B) represents the location of the nest, (C) represents the marker held horizontal to the ground and (D) represents the ruler held perpendicular to the ground 20 cm from the nest.

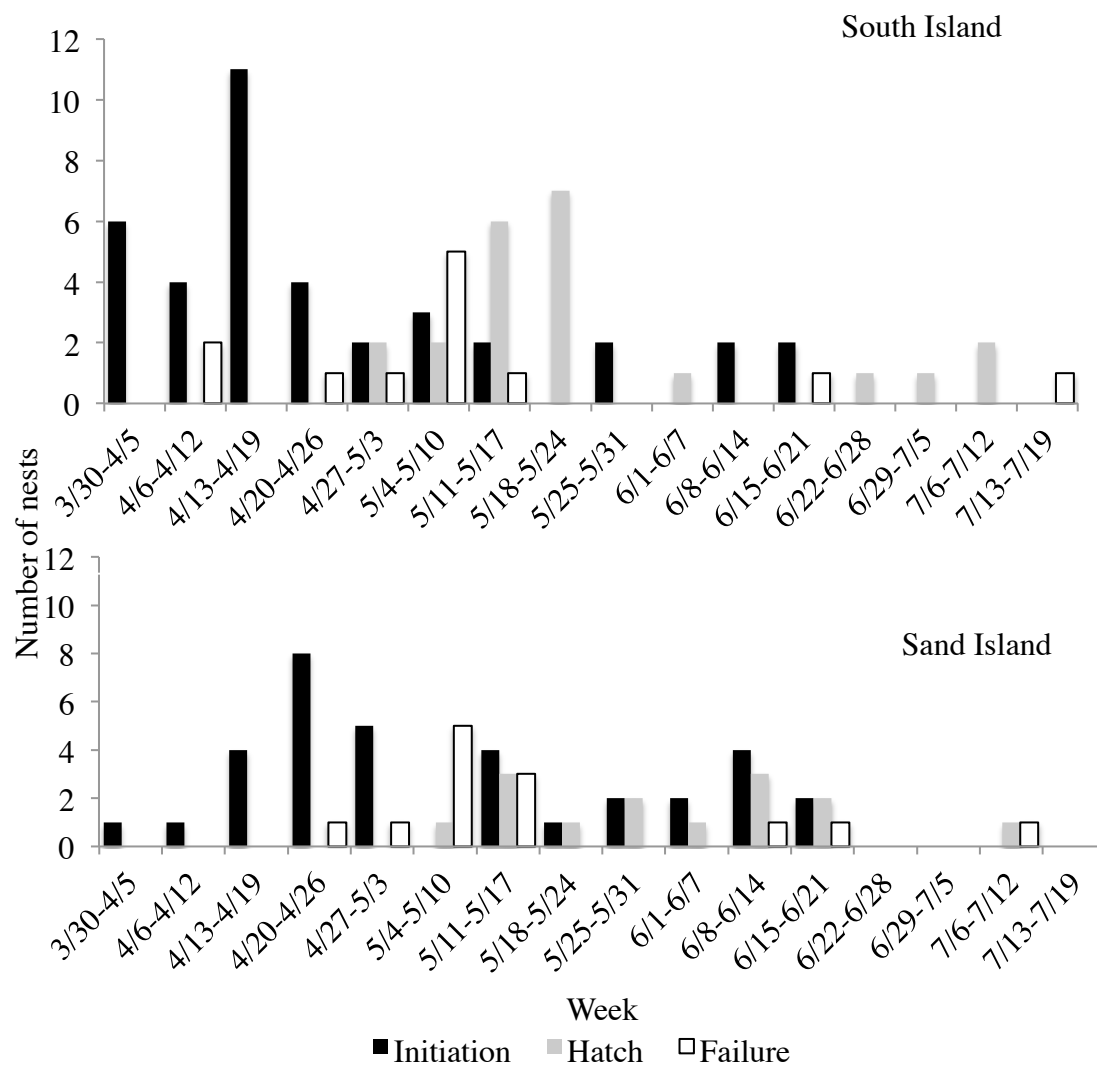


Figure 3. Number of nests initiated, hatched and failed by week for Wilson's Plovers nesting at Yawkey Center, South Carolina, USA, March – July 2012 and 2013. Data for both years are combined for each week.

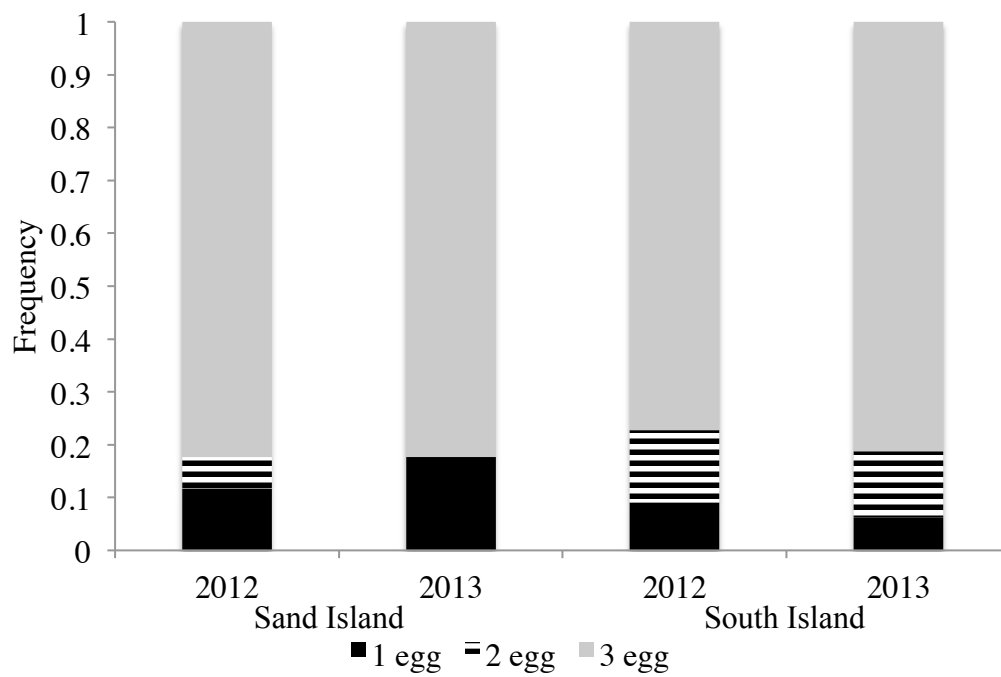


Figure 4. Clutch sizes of Wilson Plovers nesting at Yawkey Center, South Carolina, USA, March – July 2012 and 2013.

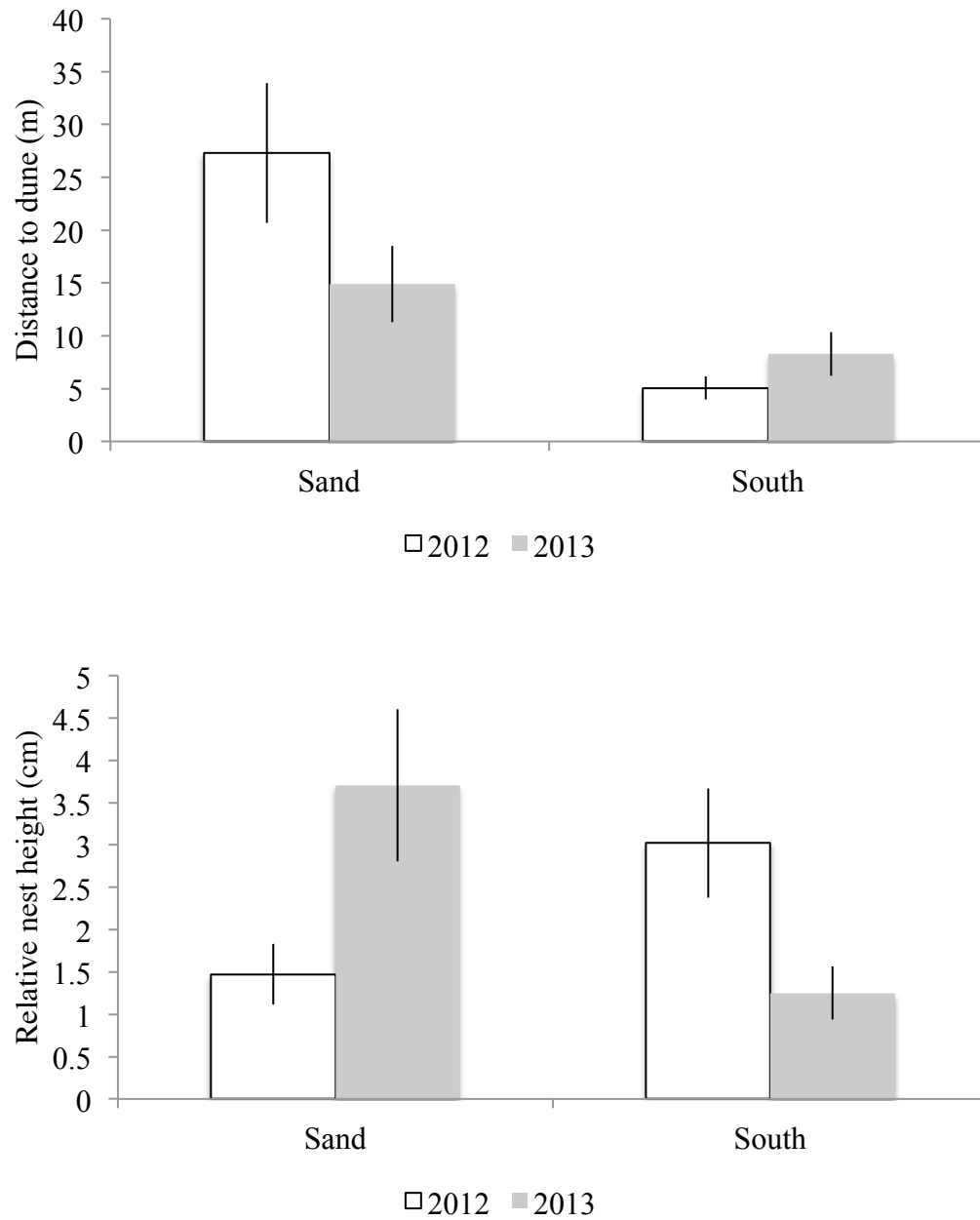


Figure 5. Distance from nest site to nearest dune and relative nest height (i.e., height of nest relative to surrounding ground) for Wilson’s Plovers, Yawkey Center, South Carolina, USA, March – July, 2012 and 2013. Bars are mean \pm 1 SE.

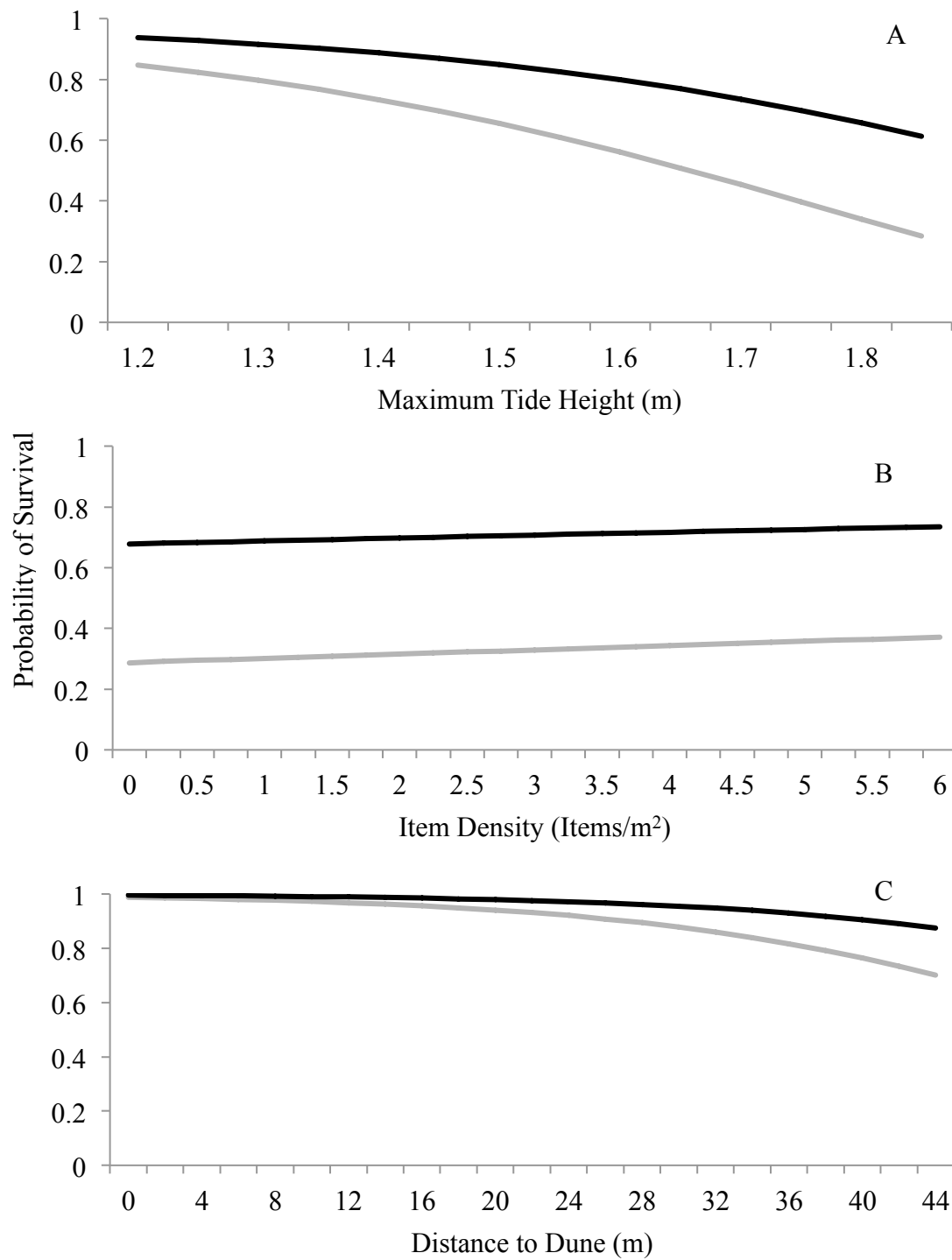


Figure 6. Probability of survival across the incubation interval for Wilson's Plovers on South Island, Yawkey Center, South Carolina, USA, March - July 2012 and

2013. Survival probability calculated using results of logistic exposure model. Panel 1- Item density and Distance to dune set at mean, maximum tide height varied from 1.2 m to 1.85 m on 0.5 m intervals. Panel 2- Maximum Tide height and distance to dune held constant at mean, Item density varied from 0 items/m² to 6 items/m² on an interval of 0.25 items/m². Panel 3- Maximum tide height and item density held constant, distance to dune varied from 1 m to 44 m on 2 m intervals. 2012 represented by grey line. 2013 represented by black line.

Table 1. Nesting chronology for Wilson's Plovers, Yawkey Center, South Carolina, USA, March – July 2012 and 2013.

	Average Initiation Date	Average Hatch Date	Average Failure Date	Earliest Nest	Last Hatch
South Island 2012	20 April	15 May	12 May	30 March	10 July
South Island 2013	1 May	31 May	15 May	7 April	11 July
Sand Island 2012	5 May	3 June	19 May	2 April	10 July
Sand Island 2013	16 May	6 June	10 June	20 April	19 June
Overall average	3 May	28 May	22 May	March 30	11 July

Table 2. Plant presence and absence at nest sites and unused sites on Sand Island at Yawkey Center during 2012 and 2013. Data for 2012 and 2013 are pooled.

		Unused Site	
		Plants	No Plants
Nest Site	Plants	0	10
	No Plants	0	20

Table 3. Item presence and absence at nest sites and unused sites on South Island at Yawkey Center during 2012 and 2013. Data are pooled for 2012 and 2013.

		Unused Site	
Nest Site	Items	Items	No Items
	No Items	3	2

Table 4. Mean values for parameters that differed significantly between used nest sites and unused sites at Yawkey Center during 2012 and 2013. Relative nest height was tested by sign test, all other variables were tested using a paired t-test. Standard errors are included in parentheses. * indicates a significant difference.

Island	Parameter	Nest Site	Paired unused site	P-value
South Island	Item Density (items/m ²)*	17.8 (2.5)	8.76 (2.6)	0.01
	Plant Density (plants/m ²)	9.0 (3.4)	4.11 (1.4)	0.93
	Distance to Vegetation (cm)*	335.9 (37.2)	95.4 (32.1)	<0.01
	Plant Height (cm)	68.4 (5.63)	59.6 (8.4)	0.32
	Distance to High Tide Line (cm)	4409 (551.8)	4323 (492.0)	0.81
	Distance to Dune (cm)	640.8 (141.7)	576.8 (125.3)	0.33
	Relative Nest Height (cm)*	2.3 (0.4)	0 (0)	<0.01
Sand Island	Item Density	4.9 (2.4)	4.12 (2.6)	0.51

(items/m ²)			
Plant Density	5.3 (1.9)	1 (1.00)	0.07
(plants/m ²)*			
Distance to	607.9 (96.3)	737.9 (104.1)	0.17
vegetation (cm)			
Vegetation	48.0 (5.5)	60.6 (6.2)	0.01
Height (cm)*			
Distance to	4819 (520.7)	4576 (478.2)	0.15
High Tide Line			
(cm)			
Distance to	2108 (308.6)	2113 (301.6)	0.96
Dune (cm)			
Relative Nest	2.6 (0.5)	0 (0)	<0.01
Height (cm)*			

Table 5. Causes of nest loss of Wilson’s Plovers at Yawkey Center, South Carolina, USA March - July 2012 and 2013. Bold numbers indicate primary cause of nest loss for a given site and year.

Site	Year	Nest failures	Numbers of Nests Lost				
			Flooding	Predation	Abandoned	Unknown	Other
South	2012	11	5	3	2	1	0
Island	2013	6	0	3	2	0	1
Sand	2012	11	3	2	0	5	1
Island	2013	9	6	3	0	0	0

Table 6. Significant coefficients from logistic exposure models for Wilson’s Plovers nesting at Yawkey Center, South Carolina, USA, March – July 2012 and 2013. Values in parentheses are standard errors.

	Variable	Estimate	Pr>ChiSq
South Island	Intercept	9.78 (3.16)	<0.01
	Year	-1.27 (0.67)	0.06
	Maximum Tide Height (m)	-3.15 (1.86)	0.01
	Distance to dune (m)	-0.08 (0.03)	0.09
	Item Density (items/m ²)	0.04 (0.02)	0.08
Sand Island	Intercept	3.43 (0.24)	<0.01

Table 7. Daily survival rate (DSR) and probability of survival for nests of Wilson's Plovers at Yawkey Center, 2012 and 2013. Standard deviations are included in parentheses. Probability of success is calculated by raising DSR by the number of days included in the laying and incubation periods (29-30 days). DSR was calculated using the coefficients and standard errors from the survival models.

Island	Variable	DSR	Probability of Survival
South Island	2012	0.977 (0.02)	0.561 (0.20)
	2013	0.988 (0.02)	0.764 (0.20)
Sand Island	N/A	0.969 (<0.01)	0.405 (0.02)

APPENDICES

Appendix 1. Initiation date, fate, and location for all Wilson's Plover nests at Yawkey Center March- July 2012 and 2013.

Nest ID	Site	Initiation Date	Fate	Latitude	Longitude	Cause of Failure
SND1201	Sand	4/04/12	Hatched	33.1787	79.1907	
SND1202	Sand	4/10/12	Hatched	33.1796	79.1905	
SND1203	Sand	4/11/12	Failed	33.1770	79.1920	Flooded
SND1204	Sand	4/16/12	Hatched	33.1790	79.1907	
SND1205	Sand	4/16/12	Failed	33.1813	79.1892	Unknown
SND1206	Sand	4/20/12	Failed	33.1797	79.1904	Unknown
SND1207	Sand	4/18/12	Failed	33.1832	79.1885	Unknown
SND1208	Sand	4/18/12	Hatched	33.1811	79.1896	
SND1209	Sand	4/23/12	Failed	33.1813	79.1892	Predated
SND1210	Sand	4/23/12	Failed	33.1844	79.1872	Predated
SND1211	Sand	4/27/12	Failed	33.1767	79.1856	Flooded
SND1212	Sand	5/29/12	Failed	33.1783	79.1914	Flooded
SND1213	Sand	6/4/12	Failed	33.1800	79.1900	
SND1214	Sand	6/12/12	Failed	33.1869	79.1861	Sea Turtle
SND1215	Sand	6/20/12	Failed	33.1795	79.1906	Unknown
SND1216	Sand	6/18/12	Hatched	33.1812	79.1897	
SND1217	Sand	6/13/12	Hatched	33.1902	79.1836	
SND1301	Sand	4/20/13	Failed	33.1811	79.1895	Flooded
SND1302	Sand	4/26/13	Failed	33.1764	79.1917	Flooded
SND1303	Sand	4/20/13	Hatched	33.1821	79.1891	
SND1304	Sand	5/11/13	Hatched	33.1768	79.1921	
SND1305	Sand	4/29/13	Hatched	33.1802	79.1906	
SND1306	Sand	5/11/13	Hatched	33.1813	79.1898	
SND1307	Sand	5/3/13	Hatched	33.1821	79.1891	
SND1308	Sand	17/05/13	Hatched	33.1880	79.1852	Predated
SND1309	Sand	5/20/13	Hatched	33.1898	79.1841	
SND1310	Sand	5/13/13	Hatched	33.1835	79.1880	
SND1311	Sand	5/26/13	Failed	33.1860	79.1870	
SND1312	Sand	4/29/13	Hatched	33.1882	79.1850	
SND1313	Sand	6/7/13	Failed	33.1845	79.1875	Flooded
SND1314	Sand	6/9/13	Failed	33.1809	79.1900	Predated
SND1315	Sand	6/15/13	Failed	33.1888	79.1847	Flooded
SND1316	Sand	6/15/13	Failed	33.1839	79.1880	Flooded
SND1317	Sand	5/30/13	Failed	33.1809	79.1892	Flooded
STH1201	South	3/30/12	Failed	33.1360	79.2402	Flooded
STH1202	South	3/31/12	Failed	33.1446	79.2292	Abandoned
STH1203	South	4/1/12	Hatched	33.1432	79.2300	

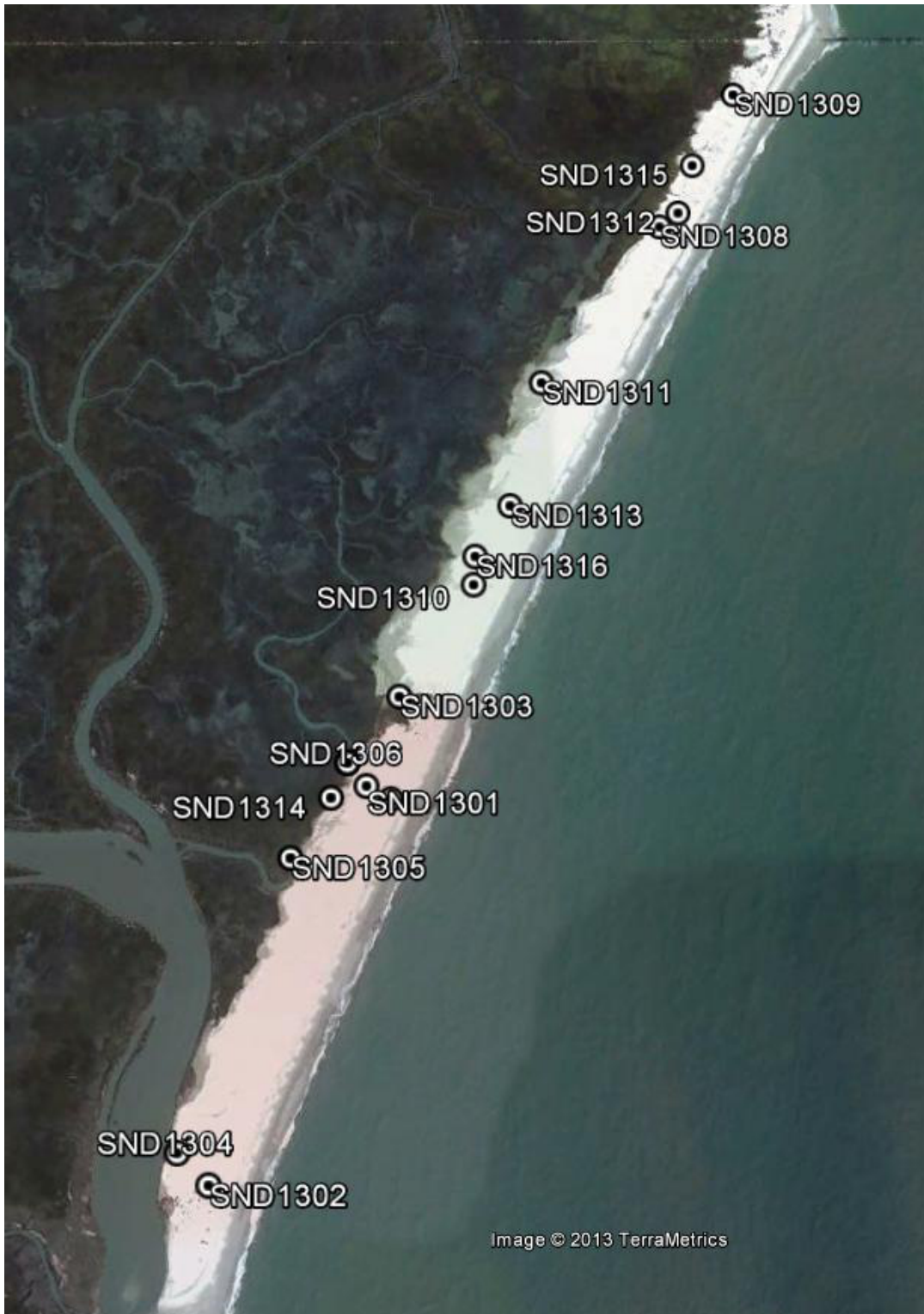
STH1204	South	4/5/12	Hatched	33.1348	79.2392	
STH1205	South	4/3/12	Failed	33.1356	79.2402	Flooded
STH1206	South	4/5/12	Hatched	33.1370	79.2405	
STH1207	South	4/6/12	Failed	33.1462	79.2274	Abandoned
STH1208	South	4/9/12	Hatched	33.1349	79.2406	
STH1209	South	4/12/12	Hatched	33.1500	79.2232	
STH1210	South	4/14/12	Failed	33.1494	79.2241	Predated
STH1211	South	4/14/12	Failed	33.1383	79.2339	Flooded
STH1212	South	4/16/12	Hatched	33.1695	79.1966	
STH1213	South	4/14/12	Hatched	33.1424	79.2307	
STH1214	South	4/16/12	Failed	33.1347	79.2392	Flooded
STH1215	South	4/17/12	Hatched	33.1454	79.2282	
STH1216	South	4/22/12	Failed	33.1352	79.2374	Flooded
STH1217	South	4/17/12	Hatched	33.1349	79.2385	
STH1218	South	4/26/12	Failed	33.1352	79.2396	Predated
STH1219	South	4/24/12	Hatched	33.1344	79.2399	
STH1220	South	6/7/12	Hatched	33.1586	79.2115	
STH1221	South	6/17/12	Failed	33.1347	79.2388	Predated
STH1222	South	6/20/12	Failed	33.1348	79.2388	Abandoned
STH1301	South	4/7/13	Failed	33.1450	79.2286	
STH1302	South	4/9/13	Hatched	33.1424	79.2307	Buried by wind
STH1303	South	4/18/13	Hatched	33.1387	79.2340	
STH1304	South	4/18/13	Hatched	33.1349	79.2377	
STH1305	South	4/16/13	Hatched	33.1698	79.1961	
STH1306	South	4/23/13	Failed	33.1357	79.2363	Abandoned
STH1307	South	4/17/13	Hatched	33.1340	79.2386	
STH1308	South	4/24/13	Hatched	33.1371	79.2405	
STH1309	South	4/19/13	Hatched	33.1373	79.2405	
STH1310	South	5/10/13	Failed	33.1647	79.2031	Predated
STH1311	South	5/4/13	Hatched	33.1544	79.2177	Predated
STH1312	South	5/13/13	Failed	33.1357	79.2403	Abandoned
STH1313	South	5/13/13	Failed	33.1347	79.2386	Predated
STH1314	South	5/27/13	Hatched	33.1353	79.2397	
STH1315	South	5/26/13	Hatched	33.1358	79.2406	
STH1316	South	6/10/13	Hatched	33.1352	79.2385	

Appendix 2. Nest locations for Wilson's Plovers at Yawkey Center from March-July 2012 and 2013. Nest codes are identical to codes listed in Appendix 1. Panel 1 represents Sand Island 2012. Panel 2 represents Sand Island 2013. Panel 3 represents South Island 2012. Panel 3 represents the southern tip of South Island 2012. Panel 4 represents South Island 2013. Panel 5 represents the southern tip of South Island 2013. (Google Earth 2013).

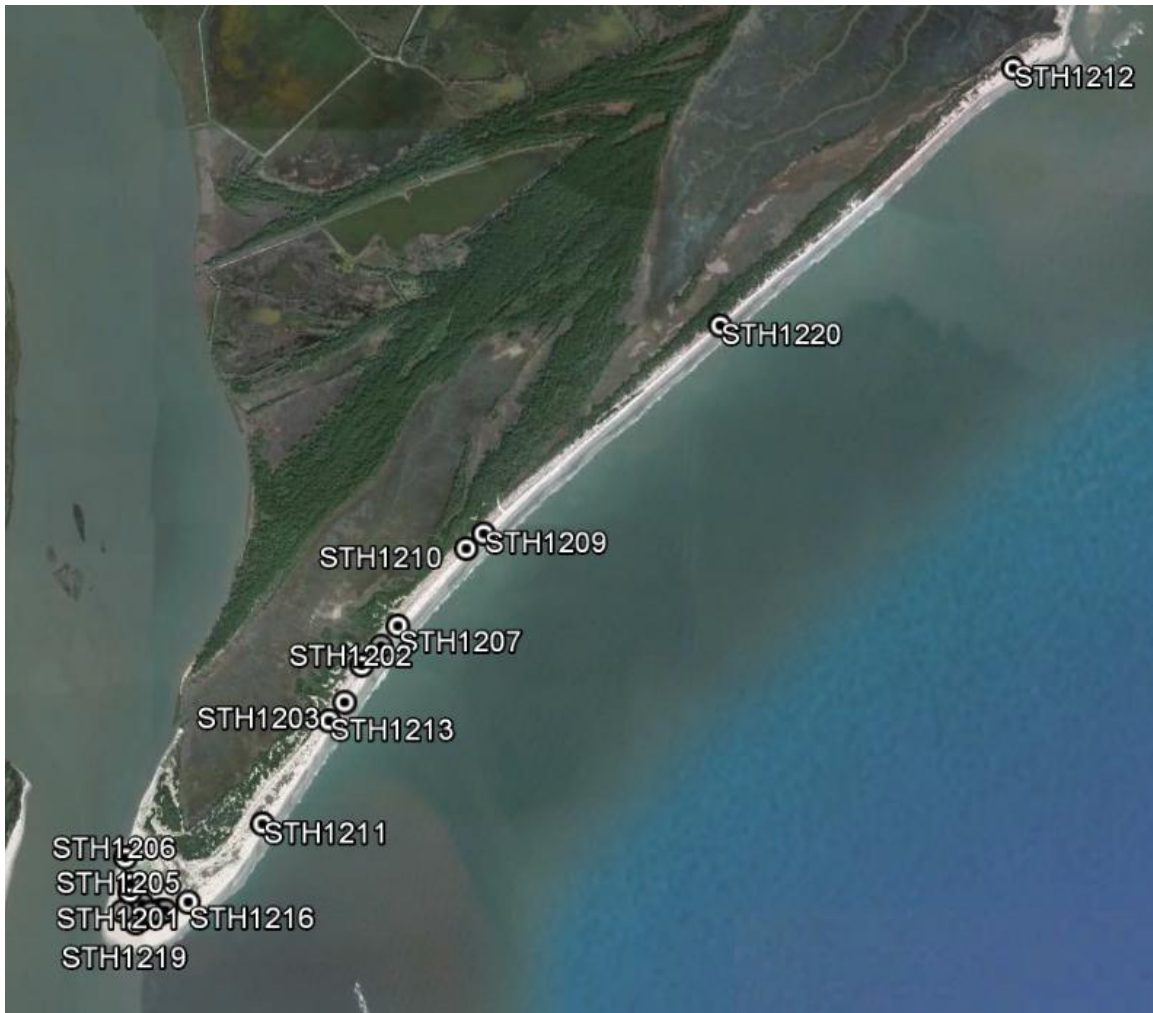
Panel 1.



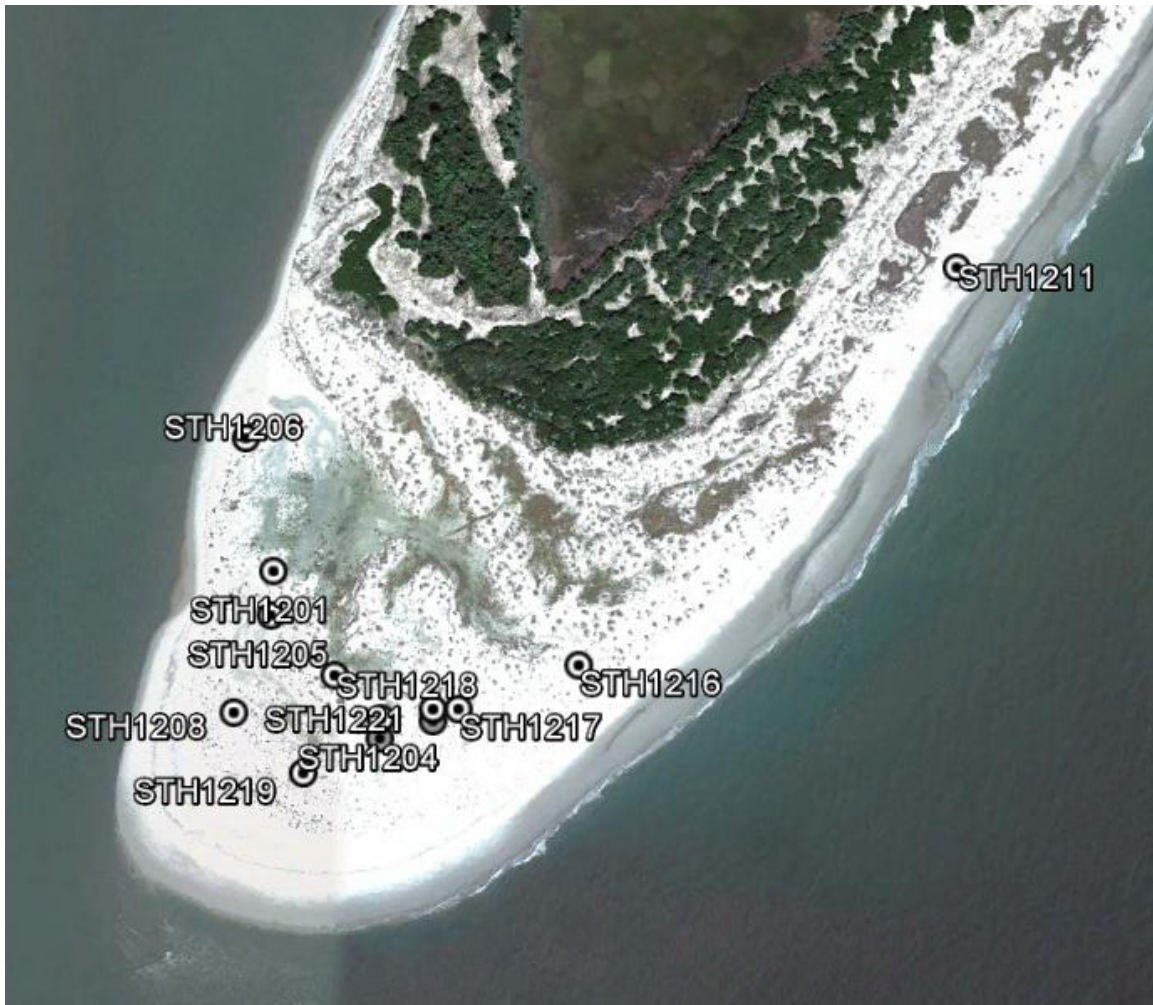
Panel 2.



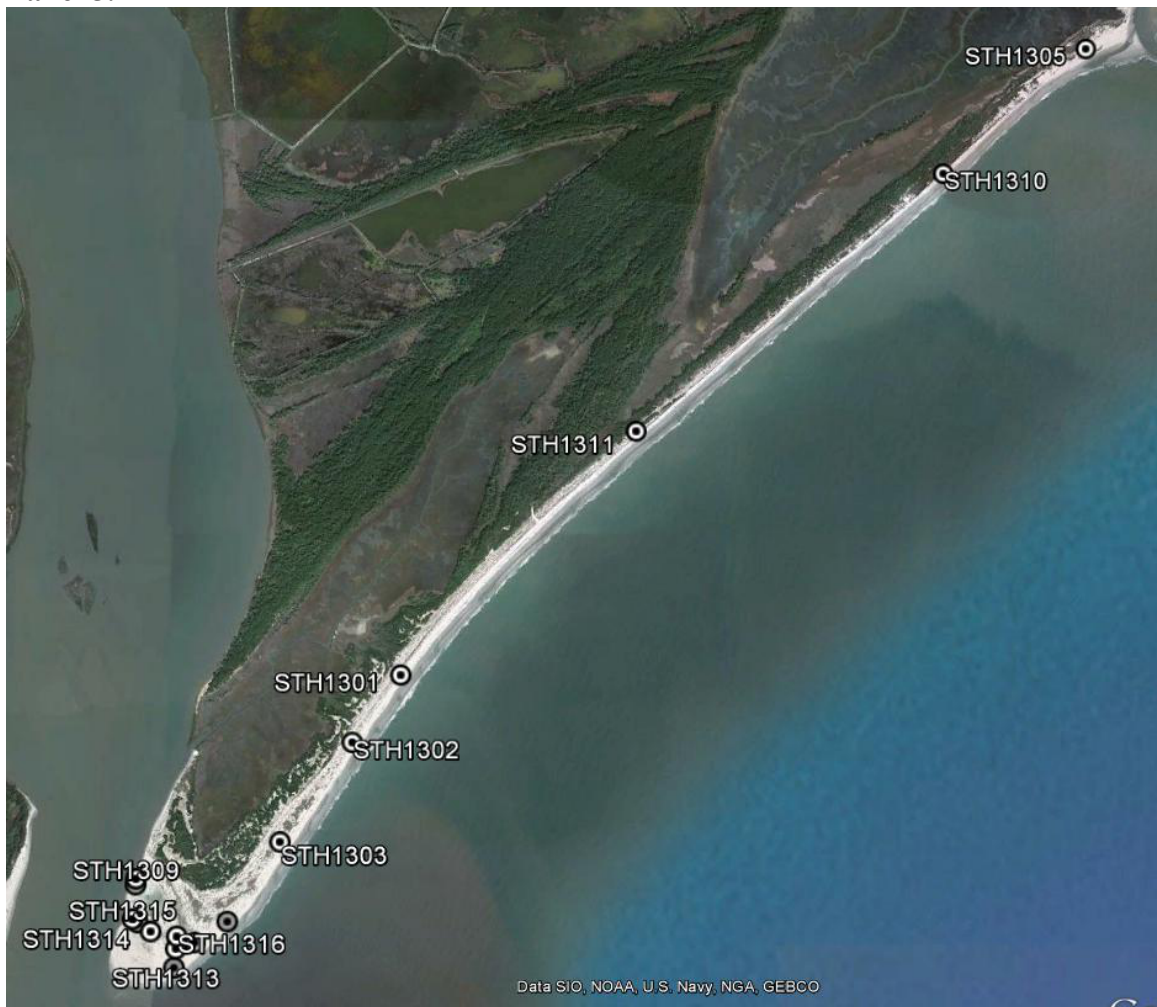
Panel 3.



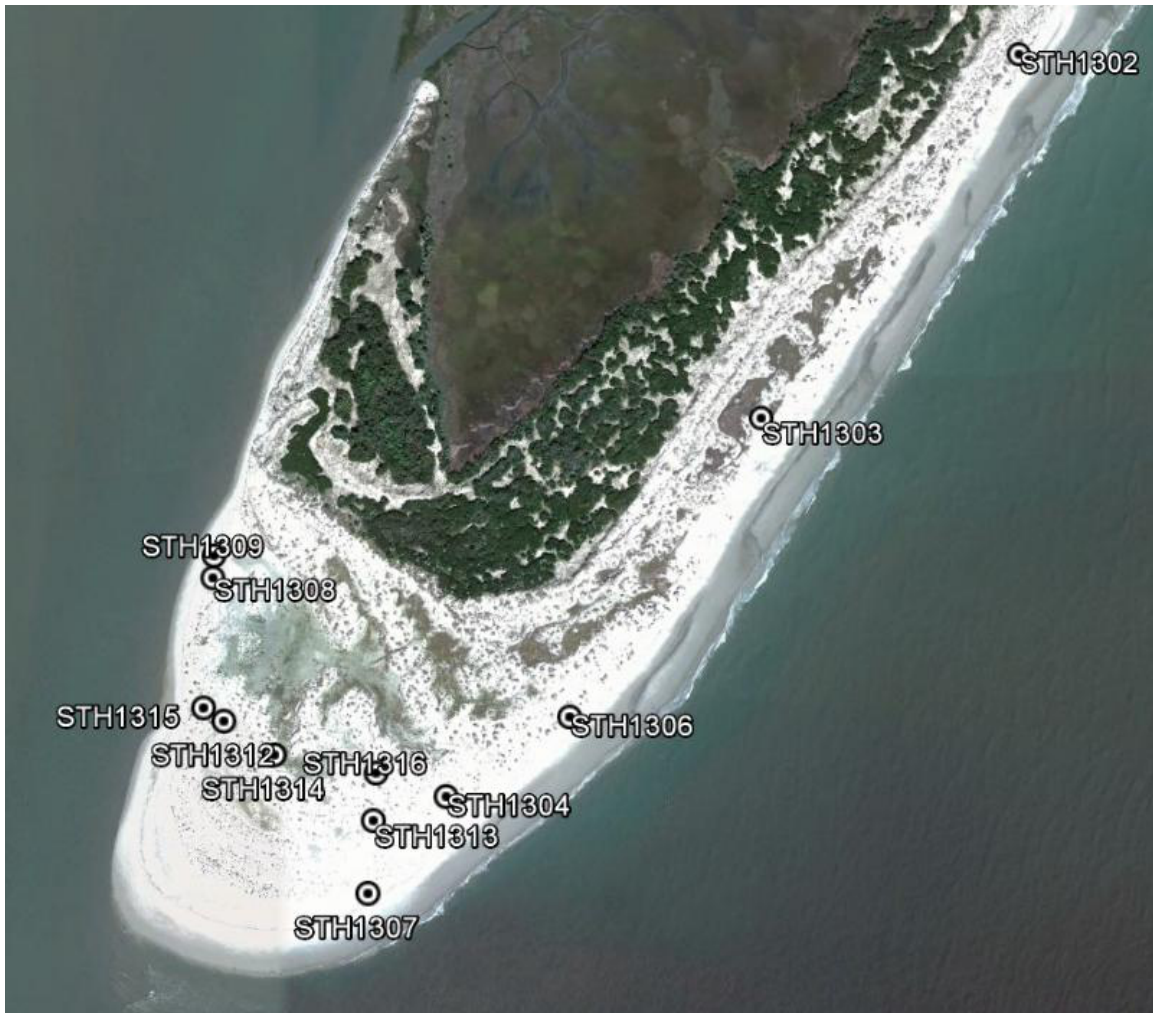
Panel 4.



Panel 5.



Panel 6.



LITERATURE CITED

- Amat, J. A., J. A. Masero. 2004. Predation risk on incubating adults constrains the choice of thermally favorable nest sites in a plover. *Animal Behavior* 67: 293-300.
- Anteau, M. J., T. L. Shaffer, M. H. Sherfy, M. A. Sovada, J. H. Stucker, and M. T. Wiltermuth. 2012. Nest survival of Piping Plovers at a dynamic reservoir indicates and ecological trap for a threatened population. *Oecologia* 170: 1167-1179.
- Bergstrom, P. W. 1988. Breeding biology of Wilson's Plovers (*Charadrius wilsonia*). *Wilson Bulletin* 100: 25-35.
- Brindock, K., A. C. Brown. 2011. Breeding success and nest site selection by a Caribbean population of Wilson's Plovers. *The Wilson Journal of Ornithology* 123: 814-819.
- Brooks G. L. 2011. Factors influencing reproductive success of near-shore seabirds in Cape Romain National Wildlife Refuge, South Carolina. M. Sc. Thesis, Clemson University, Clemson, South Carolina.
- Brooks, G. L., F. J. Sanders, P. D. Gerard, and P. G. R. Jodice. 2013. Daily survival rate for nests and chicks of Least Terns (*Sternula antillarum*) at natural nest sites in South Carolina. *Waterbirds* 36: 1-10.
- Brown, S., C. Hickey, B. Harrington, and R. Gill, eds. 2001. United States Shorebird Conservation Plan, Second edition. Manomet, MA. Manomet Center for Conservation Sciences. 70 p. <http://www.manomet.org/usscp/index.htm>.
- Burger, J. 1987. Physical and social determinants of nest-site selection in Piping Plover in New Jersey. *The Condor* 89: 811-818.
- Burger, J., and M. Gochfeld. 1990. Nest site selection in Least Terns (*Sternula antillarum*). *Colonial Waterbirds* 13: 31-40.
- Burney, C. 2009. Florida beach-nesting bird report, 2005-2008. Florida Fish and Wildlife Conservation Commission. http://www.flshorebirdalliance.org/pdf/2005-2008_FWC_BNB_report.pdf.
- Cohen, J. B., L. M. Houghton, M. Lawrence, and J. D. Fraser. 2009. Nesting density and reproductive success of Piping Plovers in response to storm- and human-created habitat changes. *Wildlife Monographs* 173: 1-24.
- Colwell, M. A., and L. W. Oring. 1990. Nest-site characteristics of prairie shorebirds. *The Canadian Journal of Zoology* 68: 297-302.
- Compton, B. W., J. M. Rhymer, and M. McCollough. 2002. Habitat selection by wood turtles (*Clemmys insculpta*): an application of paired logistic regression. *Ecology* 83: 833-843.
- Corbat, C. 1990. Nesting ecology of selected beach-nesting birds in Georgia. Ph.D. dissertation, University of Georgia, Athens, Georgia.
- Corbat, C. A., and P. W. Bergstrom. 2000. Wilson's Plover (*Charadrius wilsonia*), *The Birds of North America On Line* (A. Poole, Ed.) Ithaca: Cornell Lab of Ornithology; Retrieved from The Birds of North America Online.

- <http://bna.birds.cornell.edu.libproxy.clemson.edu/bna/species/516>.
<http://dx.doi.org.libproxy.clemson.edu/10.2173/bna.516>
- Dikun, K. A. 2008. Nest-site selection of Wilson's Plovers (*Charadrius wilsonia*) in South Carolina. M. Sc. Thesis, Coastal Carolina University, Conway, South Carolina.
- Dinsmore, S. J., M. B. Wunder, V. J. Dreitz, and F. L. Knopf. 2010. An assessment of factors affecting the population growth of the Mountain Plover. *Avian Conservation and Ecology* 5.
- Erwin, R. M., B. R. Truitt, and J. E. Jimez. 2001. Ground-nesting waterbirds and mammalian carnivores in the Virginia Barrier Island Region: Running out of options. *Journal of Coastal Research* 17: 292-296.
- Fedy, B., and K. Martin. 2011. The influence of fine-scale habitat features on regional variation in population performance of alpine White-tailed Ptarmigan. *Condor* 113: 306-315.
- Georgia Department of Natural Resources. 2010. Wilson's Plover upswing- census of these birds shows increase in nesting pairs. <http://www.georgiawildlife>
- Greenwald, K. R. 2009. Nest lining and fledging success in the Piping Plover are related to nest site characteristics. *Waterbirds* 32: 464-467.
- Gochfeld, M., and J. Burger. 1994. Black Skimmer (*Rynchops niger*), *The Birds of North America On Line* (A. Poole, Ed.) Ithaca: Cornell Lab of Ornithology; Retrieved from *The Birds of North America Online*.
<http://bna.birds.cornell.edu.libproxy.clemson.edu/bna/species/108>.
<http://dx.doi.org.libproxy.clemson.edu/10.2173/bna.108>.
- Google Inc. (2013). Google Earth (Version 7.0.3.8542) [Software].
- Houston, A., and S. Cameron. 2008. Coastal region waterbird investigations and annual report. North Carolina Wildlife Resources Commission, Wildlife Diversity Program.
- Hughes, T. P. 1990. Limitation, mortality, and population regulation in open systems: a case study. *Ecology* 71: 12-20.
- Hunter, C. C. 2002. Southeastern coastal plains-Caribbean region report. U.S. Shorebird Conservation Plan. U. S. Fish and Wildlife Service. Georgia.
- Jodice, P. G. R., T. Murphy, F. Sanders, and L. M. Ferguson. 2007. Longterm trends in nest counts of colonial nesting shorebirds in South Carolina, USA. *Waterbirds* 30: 40-51.
- Julliard, R. 2004. Estimating the contribution of survival and recruitment to large scale population dynamics. *Animal and Biodiversity Conservation* 27: 417-426.
- Kolar, M., and K. Withers. 2004. Census of Snowy and Wilson's Plover on the Texas coast. http://ccs.tamucc.edu/pubs/tech/TAMUCC_0403_CCS.pdf.
- Lloyd, J. D., and J. J. Tewksbury. 2007. Analyzing avian nest survival in forests and grasslands: a comparison of the Mayfield and logistic-exposure methods. *Studies in Avian Biology* 34: 96-104.
- Mabee, T. J., A. M. Wildman, and C. B. Johnson. 2006. Using egg flotation and eggshell evidence to determine age and fate of Arctic shorebird nests. *Journal of Field Ornithology* 77:163-172.

- Medieros, R., J. A. Ramos, P. Pedro, and R. J. Thomas. 2012. Reproductive consequences of nest site selection by little terns breeding on sandy beaches. *Waterbirds* 35: 512-524.
- Miller, E. H., and M. J. Jordan. 2011. Relationship between exotic invasive shrubs and American Woodcock (*Scolopax minor*) nest success and habitat selection. *Journal of the Pennsylvania Academy of Science* 85:132-139.
- Norris, K., P. W. Atkinson, and J. A. Gill. 2004. Climate change and coastal waterbird populations- past declines and future impacts. *Ibis* 146: 82-89.
- Nol, E., and R. C. Humphrey. 2012. American Oystercatcher (*Haematopus palliatus*), *The Birds of North America On Line* (A. Poole, Ed.) Ithaca: Cornell Lab of Ornithology; Retrieved from *The Birds of North America Online*.
<http://bna.birds.cornell.edu/libproxy.clemson.edu/bna/species/082>.
<http://dx.doi.org/libproxy.clemson.edu/10.2173/bna.082>.
- Page, G. W., L. E. Stenzel, and C. A. Ribic. 1985. Nest site selection and clutch predation in the snowy plover. *Auk* 102: 347-353.
- Patten, M. A., D. H. Wolfe, E. Shochat, and S. K. Sherrod. 2005. Effects of microhabitat and microclimate on adult survivorship of the lesser prairie-chicken. *Journal of Wildlife Management* 69: 1270-1278.
- Norris, K., P. W. Atkinson, and J. A. Gill. 2004. Climate change and coastal waterbird populations- past declines and future impacts. *Ibis* 146: 82-89.
- Nguyen, L. P., E. Nol, and K. F. Abraham. 2003. Nest success and habitat selection of the Semipalmated Plover on Akimiski Island, Nunavut. *Wilson Bulletin* 115: 285-291.
- Ray, K. L. 2011. Factors affecting Wilson's Plover (*Charadrius wilsonia*) demography and habitat use at Onslow Beach, Marine Corps base Camp Lejeune, North Carolina. M. Sc. thesis, Virginia Polytechnic Institute and State University, Blacksburg, Virginia.
- Saalfeld, S. T., W. C. Conway, D. A. Haukos, and W. P. Johnson. 2012. Nest success of Snowy Plovers (*Charadrius nivosus*) in the Southern High Plains of Texas. *Waterbirds* 34: 389-399.
- Saether, B., V. Grotan, S. Engen, D. G. Noble and R. P. Freckleton. 2009. Critical parameters for predicting population fluctuations of some British passerines. *Journal of Animal Ecology* 78: 1063-1075.
- Sanders, F.J., M. Martin, M. D. Spinks, and N. J. Wallover. 2013. Abundance and breeding distribution of Wilson's Plovers during the breeding season in South Carolina. *The Chat* 76: 117-124.
- Schaffer, T. L. 2004. A unified approach to analyzing nest success. *Auk* 121: 526-540.
- Smith, P. A., H. G. Gilchrist, and J. N. M. Smith. 2007. Effects of nest habitat, food and parental behavior on shorebird nest success. *Condor* 109:15-31.
- Smith, C., A. Wilke, and R. Boettcher. 2009. Virginia Plover Summary.
<http://ebird.org/content/va/news/2009-virginia-plover-summary>.
- Smith, P. A., I. Tulp, H. Schekkerman, H. G. Gilchrist, and M. R. Forbes. 2012. Shorebird incubation behavior and its influence on the risk of nest predation. *Animal Behavior* 84: 835-842.

- Tremblay, J. P., G. Gauthier, D. Lepage, and A. Desrochers. 1997. Factors affecting nesting success in Greater Snow Geese: Effects of habitat and association with Snowy Owls. *Wilson Bulletin* 109: 449-461.
- Thibault, J. M. 2008. Breeding and foraging ecology of American Oystercatchers in the Cape Romain Region, South Carolina. M. Sc. Thesis, Clemson University, Clemson, South Carolina.
- Thompson, B. C., J. A. Jackson, J. Burger, L. A. Hill, E. M. Kirsch, and J. L. Atwood. 1997. Least Tern (*Sternula antillarum*), *The Birds of North America On Line* (A. Poole, Ed.) Ithaca: Cornell Lab of Ornithology; Retrieved from *The Birds of North America Online*.
<http://bna.birds.cornell.edu.libproxy.clemson.edu/bna/species/290>.
<http://dx.doi.org.libproxy.clemson.edu/10.2173/bna.290>.
- Tomkins, I. R. 1944. Wilson's Plover in its Summer House. *Auk* 61:259-269.
- Williams, G. E., and P. B. Wood. 2002. Are traditional methods of determining nest predators and nest fates reliable? An experiment with wood thrushes (*Hylocichla mustelina*) using miniature video cameras. *Auk* 119: 1126-1132
- Zdravkovic, M. 2005. 2004 Coastal Texas Breeding Snowy and Wilson's Plover Census and Report, Coastal Bird Conservation Program, National Audubon Society, Science Dept. New York, NY.
- Zdravkovic, M. 2010. Wilson's Plover (*Charadrius wilsonia*) breeding biology study at select sites in coastal Louisiana, 2009 Breeding summary report, Coastal Bird Conservation Program Conservian, Big Pine Key, Florida. Submitted to Barataria-Terrebonne National Estuary Program, Thibodaux LA.
- Zdravkovic, M. G. 2013. Conservation plan for the Wilson's Plover (*Charadrius wilsonia*) Version 1.0. Manomet Center for Conservation Sciences, Manomet, Massachusetts, USA.